Notes on the Biology of Australian Seagrasses*

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This contribution focuses on the anatomy, histochemistry and ultrastructure of vegetative organs of Australian seagrasses in relation to their possible functions. Detailed anatomical and ultrastructural structures vary with species. Some structures are similar to those in terrestrial plants and others are unique in seagrasses for adaptation to a marine environment. Some details of the taxonomy, distribution, habitat and life history of Australian seagrasses are also included. The structure of the phyllosphere and rhizosphere in seagrasses is discussed as well as the possible significance of the role of epiphytes and epifauna.

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INTRODUCTION

Seagrasses are aquatic angiosperms which are completely adapted to life in the marine environment. According to Arber (1920) and den Hartog (1970) they require at least the following adaptations to be able to colonize the marine environment successfully: (1) they live fully submerged in seawater, (2) they have an anchoring system, (3) they have a hydrophilous pollination, (4) they are able to cope with a high salinity. Seagrasses are abundant in Australian waters and play a significant role in marine food chains (Larkum, 1977; King, 1981; McComb *et al.*, 1981). The ecology of seagrasses including Australian species has been intensively reviewed (McRoy and Helfferich, 1977; Larkum, 1977; Phillips and McRoy, 1980; McComb *et al.*, 1981) and will not be dealt with here. Knowledge on other biological aspects of these marine vascular plants is still fragmented. This contribution, which emphasizes anatomy, cellular structure and function, is concerned with these adaptations and other biological aspects of marine angiosperms in Australian waters. A comparative leaf morphology and gross anatomy of seagrasses has been described by Tomlinson (1980).

TAXONOMY, DISTRIBUTION AND HABITATS

Taxonomy

Den Hartog (1970) contributed an excellent taxonomic study on seagrasses of the world, listing 49 species belonging to twelve genera and four families of angiosperms regarded as seagrasses. A brief taxonomic study of eastern Australian *Zostera* has been made by Jacobs and Williams (1980). A comprehensive taxonomy of temperate Australian seagrasses will be available soon (Womersley and Robinson, in preparation). Australia is well endowed with seagrasses; there are 25 described species belonging to all genera except the genus *Phyllospadix* represented in Australian waters (Table 1). Three of these species have only recently been described (Greenway, 1979; Cambridge and Kuo, 1979), and four new *Posidonia* species are to be described (Kuo and Cambridge, in preparation). Dehydrated specimens, which were collected as drift on the beach and deposited in herbaria, were used by den Hartog (1970). However, herbaria have recently received an increasing number of seagrass specimens taken from their natural habitats. Unfortunately, most herbaria have stored seagrasses in a dehydrated state and the author found it difficult to study the morphology of these dried seagrasses.

TABLE 1

The Australian Seagrasses

Genus[1]	Species	Endemic to[2] Australia	Distribution[3]	
Zosteraceae (Potamogetonaceae)				
Zostera	*capricorni* Aschers.		C	Qld., NSW
(12)	*mucronata* den Hartog	E	S	SA, WA
	muelleri Irmisch & Aschers.	E	S	SA, Tas, Vic.
Heterozostera	*tasmanica* (Martens ex Aschers.)	E	S	SA, WA, Vic.,
(1)	den Hartog			NSW, Tas.
Posidoniaceae (Potamogetonaceae)				
Posidonia	*angustifolia* Cambridge & Kuo	E	S	WA, SA
(5)	*australis* Hook F.	E	S	NSW, Vic., Tas.,
				SA, WA
	ostenfeldii den Hartog	E	S	WA, SA
	sinuosa Cambridge & Kuo	E	S	WA, SA
Cymodoceaceae (Zannichelliaceae; Potamogetonaceae)				
Halodule	*pinifolia* (Miki) den Hartog		N	Qld.
(6)	*uninervis* (Forsk.) Aschers.		N	WA, Qld.
	in Boissier			
Cymodocea	*angustata* Ostenfeld	E	N	WA
(4)	*rotundata* Ehrenb. & Hempr.		N	Qld.
	ex Aschers.			
	serrulata (R.Br.) Aschers. & Magnus		N	Qld., WA
Syringodium	*isoetifolium* (Aschers.) Dandy		C	WA, Qld.
(2)				
Thalassodendron	*ciliatum* (Forsk.) den Hartog		N	Qld.
(2)	*pachyrhizum* den Hartog	E	S	WA
Amphibolis	*antarctica* (Labill.) Sonder et	E	S	WA, SA,
(2)	Aschers.			Vic., Tas.
	griffithii (J. M. Black) den Hartog	E	S	WA, SA
Hydrocharitaceae				
Enhalus	*acoroides* (L.F.) Royle		N	Qld.
(1)				
Thalassia	*hemprichii* (Ehrenb.) Aschers.		N	Qld.
(2)				
Halophila	*decipiens* Ostenfeld		N	Qld., NSW
(9)	*ovalis* (R.Br.) Hook F.		C	WA, Vic., NSW,
				Qld., NT
	ovata Gaud. in Freycin.		N	WA, Qld.
	spinulosa (R.Br.) Aschers.		N	WA, Qld.
	tricostata Greenway	E	N	Qld.

1. Number in ( ) represents total world species in the genus. Only the genus *Phyllospadix* (5) is not represented in Australia.
2. E: species endemic to Australia.
3. N, occurring only in northern, tropical waters; S, occurring in southern, temperate waters; C, cosmopolitan, occurring in tropical and temperate waters.

   Qld., Queensland; NSW, New South Wales; Vic., Victoria; SA, South Australia; Tas., Tasmania; WA, Western Australia; NT, Northern Territory.

Distribution

A brief biogeography of Australian seagrasses has been discussed by Specht (1981). Australian seagrasses show a high degree of endemism as well as having a strong affinity with those of other continents and island groups. Half of the Australian species, and the genera *Amphibolis* and *Heterozostera*, are endemic to Australia, while some species, including *Enhalus acoroides* (L.f.) Royle, *Thalassodendron ciliatum* (Forsk.)
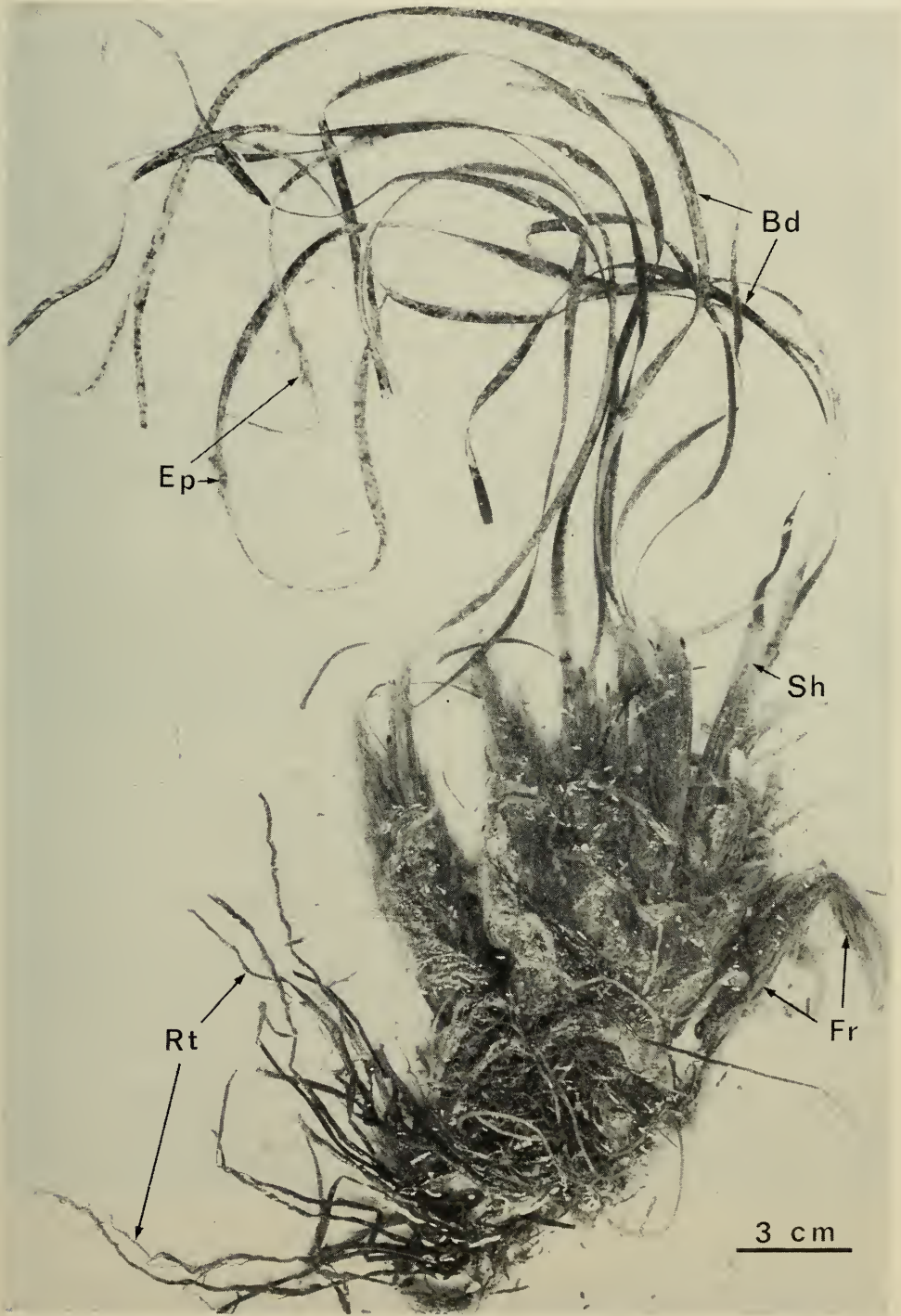
Fig. 1. A typical temperate Australian seagrass *Posidonia australis* Hook F. Bd: Leaf blade; Sh: Leaf sheath; Fr: Fibres; Rt: Roots; Ep: Epiphytes. Note the rhizome is covered by the fibres.

den Hartog, *Syringodium isoetifolium* (Aschers.) Dandy are also found elsewhere in the Indo-Pacific region. *Halophila ovalis* (R.Br.) Hook.f. has a much wider distribution. Within Australian waters, some genera (e.g. *Enhalus, Cymodocea, Halodule, Thalassia* and most species of *Halophila*) are found only in tropical areas, others (e.g. *Posidonia, Amphibolis, Heterozostera* and most species of *Zostera*) occur only in temperate waters. On the other hand, *Syringodium isoetifolium* and *Halophila ovalis* are found in both temperate and tropical waters. The latitudes 30°S on the east coast and 25°S on the west coast of Australia appear to be transition points for a great number of tropical and temperate seagrass communities (Larkum, 1977). No information is available at present on seagrasses of nothern Australia, from Port Hedland in Western Australia to the Gulf of Carpentaria in Queensland (McComb *et al.*, 1981).

Habitat

Different seagrasses grow on different substrates (den Hartog, 1970). *Halophila* is found in all kinds of habitats from open sea to estuaries and inlets. *Cymodocea, Thalassia* and *Zostera* can also be found on various substrates and the depth limit of most of the species of these genera is 10 to 12 metres. *Syringodium* is restricted usually to the upper sublittoral zone where it sometimes appears rarely to make up monospecific meadows. *Enhalus, Amphibolis, Thalassodendron* and *Posidonia* are also restricted to the upper sublittoral zone with some exceptions. In Western Australia, Cambridge (1975) found that *Thalassodendron pachyrhizum* den Hartog occurs only on limestone and granitic reefs and never on sands, and could be found to a depth of at least 40 metres. She also noticed that *Amphibolis* usually inhabits sand and sand-covered reefs as either dense meadows or small clumps, while *Posidonia ostenfeldii* den Hartog is found in sandy substrates on *unsheathed* sand banks. *Posidonia australis* Hook. f. forms vast meadows in embayments enclosed by reefs, shoals and islands. *P. australis* appears to be quite tolerant of salinity fluctuations, as it has been reported in Shark Bay where salinity can be as high as $40\frac{o}{oo}$ (Cambridge, 1979, personal communication). The largest, densest seagrass beds are found in St Vincent and Spencer Gulfs of South Australia and in Shark Bay in Western Australia. The area of the latter embayment has been estimated at more than 10,000 km^2 (Davis, 1970). There is no doubt that the most extensive seagrass community in these beds is that formed by *Posidonia* spp.

VEGETATIVE STRUCTURE AND FUNCTION

Seagrasses show a high degree of uniformity in their morpological appearance; most genera have well-developed rhizomes and linear or strap-shaped leaves, *Halophila* being the only exception. However, the anatomical structure of the seagrasses exhibits a considerable degree of diversity. Some seagrass genera are monomorphic (i.e. with shoots bearing only one kind of leaf foliage leaves, *Posidonia, Zostera, Heterozostera, Cymodocea, Halodule* and *Enhalus*) and others are dimorphic (i.e. with two types of shoot-bearing scale leaves and foliage leaves respectively, *Amphibolis, Thalassodendron, Syringodium, Halophila* and *Thalassia*). Species of *Halophila* have shoots of variable length. A typical seagrass, *P. australis* (Fig. 1), has a creeping rhizome which at each node produces two branching roots and a unit of three foliage leaves protected by a sheath at the base.

1. LEAF BLADE (Figs 2-4).

A transverse section of leaf blade (Fig. 2, **A-G**) reveals a thin cuticle covering a single cell layer of epidermis which lies above the parenchyma (mesophyll) or fibre cells (mechanical tissue). Numerous vascular bundles and air lacunae are embedded among the parenchyma cells.
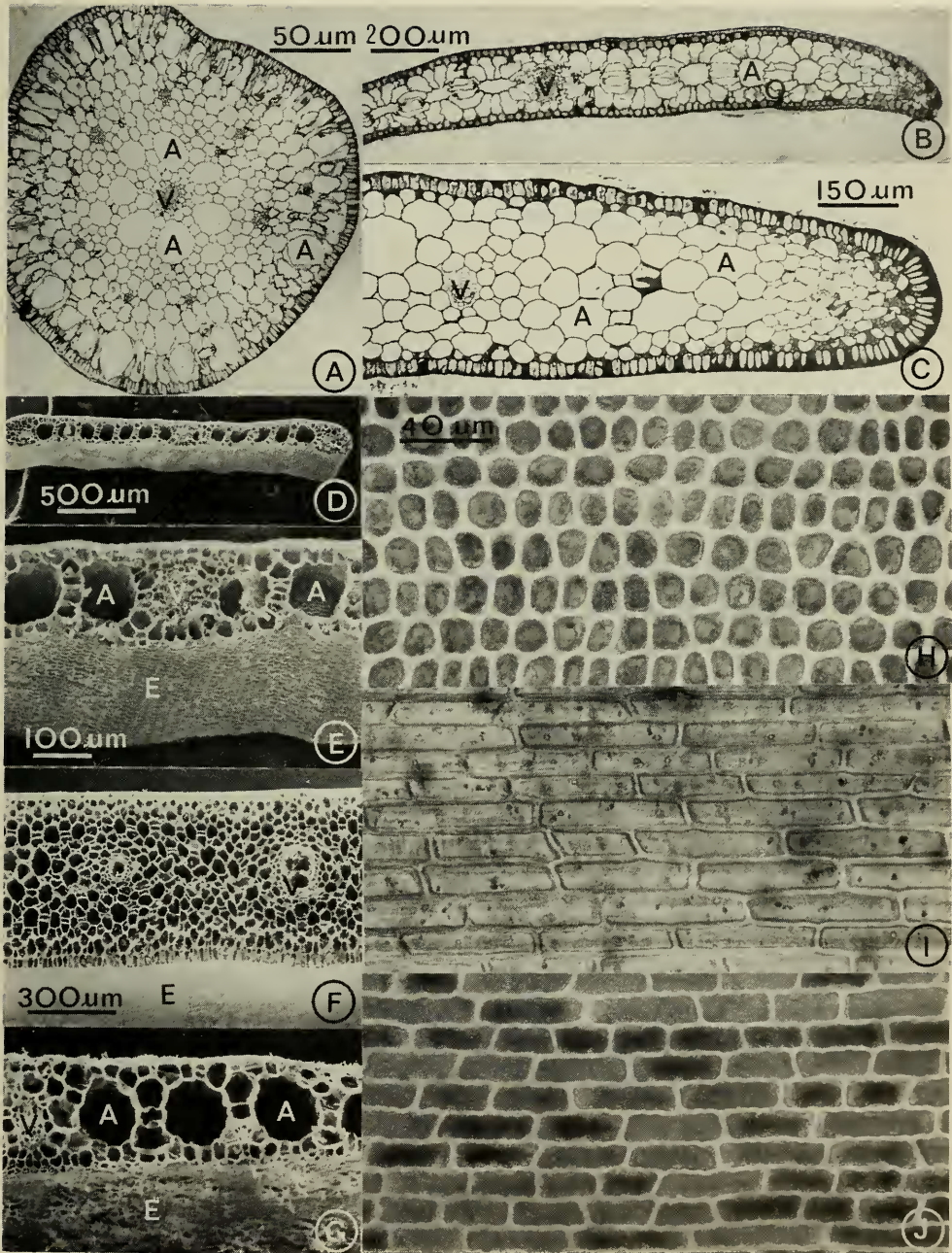
Fig. 2. The leaf blade anatomy of seagrasses and the leaf epidermal morphology of some Australian *Posidonia*.

A-G. Transverse sections of the leaf blade of **A**, *Syringodium isoetifolium;* **B**, *Zostera muelleri;* **C**, *P. australis;* **D**, *Z. muelleri* (SEM); **E**, *Heterozostera tasmanica* (SEM); **F**, *P. ostenfeldii* (SEM); **G**, *Enhalus acoroides* (SEM). A: Air-lacunae; E: Epidermis; V: Vascular bundles.

H-J. The surface view of the *Posidonia* leaf epidermis (all same magnification). **H**, *P. australis;* **I**, *P. angustifolia;* **J**, *P. sinuosa.*

Cuticle: There are no stomata in seagrasses (Doohan and Newcomb, 1976; Kuo, 1978) (Fig. 2, **H-J**). The appearance of the cuticle under electron microscopy differs among species. With the exception of *P. sinuosa* (Cambridge and Kuo, 1982) the genus *Posidonia* (Kuo, 1978; Fig. 3, **D**) has an unusual porous texture. The inner face of the cuticle has oval cavities in *Zostera muelleri* Irmisch & Aschers and *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog (Fig. 3, **F**). A similar structure has been observed in *Z. capensis* and it has been suggested that it might have an association with iron absorption, secretion and storage (Barnabas *et al.*, 1977) or might even have an excretory function (Barnabas *et al.*, 1980). The cuticle may appear as a thin, electron-transparent layer in *P. sinuosa, Thalassia hemprichii* (Ehrenb.) Aschers., *Cymodocea serrulata* (R.Br.) Aschers. & Magnus, *Cymodocea rotundata* Ehrenb. & Hempr. ex Aschers. and *Syringodium isoetifolium* (Fig. 3, **E**; Doohan and Newcomb, 1976). The cuticle has been reported as absent in the northern hemisphere *Thalassia testudinum* Banks ex König (Benedict and Scott, 1976). It is thought that the cuticle of the submerged leaves offers little resistance to carbon diffusion from surrounding water in the absence of a functional stomatal system.

Epidermal Cells: The shape of the epidermal cells is sometimes a useful taxonomic character (Cambridge and Kuo, 1979; Fig. 2, **H-J**). The thickened walls of epidermal cells are rich in pectin and celluloses but are not lignified (Kuo, 1978). Epidermal transfer cells have been observed in *Thalassia, Cymodocea, Halophila, Halodule, Zostera* (Fig. 3, **G**) and *Heterozostera* (Jagel, 1973, 1982; Birch, 1974; Doohan and Newcomb, 1976; Barnabas *et al.*, 1977; Kuo, unpublished) but are absent in *Posidonia* (Fig. 3, **H**), *Amphibolis, Syringodium* and *Thalassodendron* (Kuo, 1978; unpublished). An unusual structure has been observed in *Halophila* epidermis (Birch, 1974). Epidermal cells contain most of the leaf chloroplasts as well as numerous mitochondria, Golgi bodies and microbodies (Doohan and Newcomb, 1976; Kuo, 1978; Fig. 3, **G-H**). Phenolic materials may also occur in the epidermal cells of certain species. The epidermal cells appear to have active photosynthetic and mitochondrial metabolisms associated with osmoregulation (Jagel, 1973; 1982). These cells may be the primary site of carbon dioxide fixation and carbon dioxide uptake. The products of photosynthesis in the epidermal cells may be transported to the mesophyll cells and to the vascular systems via plasmodesmata (Kuo, 1978).

The $^{13}C/^{12}C$ ratio, measured as $\delta\ ^{13}C$ values in the range $- 3.0$ to $- 19.0\%$, have been recorded in seagrass leaves (Smith and Epstein, 1971; Doohan and Newcomb, 1976; Benedict and Scott, 1976; Andrews and Abel, 1979; McMillan *et al.*, 1980). These values are within the range usually associated with C_4 terrestrial plants that fix carbon dioxide during photosynthesis with phosphoenolpyruvate carboxylase (Smith and Epstein, 1971). The high variability in $\delta\ ^{13}C$ values might be associated with a variable photosynthesis metabolism in seagrasses (McMillan *et al.*, 1980) and it has been thought that the C_4 pathway might operate in seagrass photosynthesis (Benedict and Scott, 1976). However, recent biochemical studies of four Australian tropical seagrasses by Andrews and Abel (1979) indicate that photosynthesis occurs via the C_3 rather than the C_4 pathway. Studies of leaf anatomy, which do not show the 'Kranz' anatomy of terrestrial C_4 plants (Fig. 1, **A-C**) (Jagel, 1973; Doohan and Newcomb, 1976; Barnabas *et al.*, 1977; Kuo, 1978; Tomlinson, 1980) and of photorespiration (Hough, 1976) suggested that seagrasses may not be typical C_3 or C_4 plants. At the pH of seawater, there is more bicarbonate and less carbon dioxide available in seawater than there is in the air. Thus, it is still uncertain whether seagrasses take up carbon in carbon dioxide or bicarbonate form from surrounding water for photosynthesis (Beer *et al.*, 1977; Sand-Jensen, 1977).
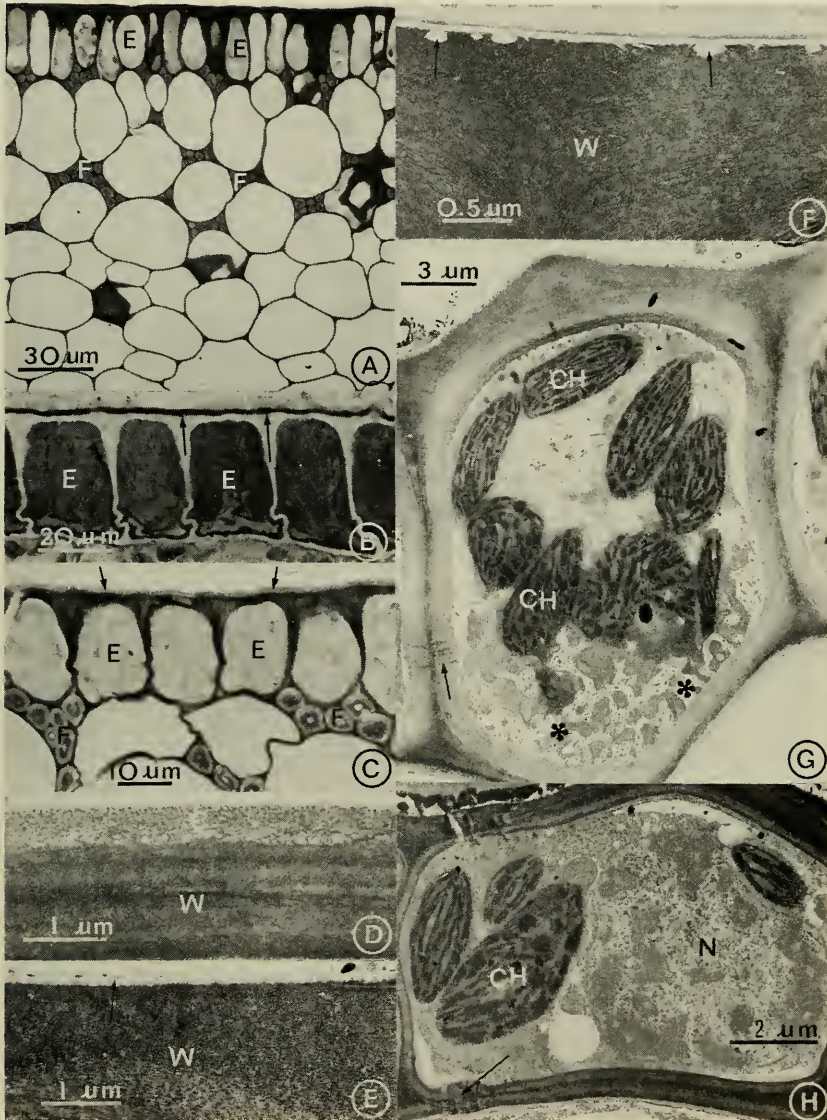
Fig. 3. The structure of the leaf epidermis and the cuticle of some Australian seagrasses.
A. The portion of the leaf blade in *P. ostenfeldii*. Note that the epidermal cells (E) contain tannins and fibre cells (F) associated with epidermal and other hypodermal cells.
B and **C.** A pronounced cuticle (arrows) covering the epidermal cells (E) of *P. australis*, sudan black and toluidine blue stained respectively.
D-F. Electron micrographs of seagrass cuticle.
D, *P. australis* cuticle (C) has a porous appearance. **E**, an electron-transparent cuticle (arrow) in *Syringodium isoetifolium*. **F**, cup-shaped invaginations (arrows) occur in the outer epidermal wall (W) of *Z. muelleri*.
G. Electron micrograph of the epidermal cell of *Z. muelleri*. Note that the cell has many chloroplasts; more cell wall ingrowths (asterisks) occur in the basal than the distal tangential walls. Some plasmadesma (arrow) are present between the epidermal cells.
H. Electron micrograph of the epidermal cell of *P. australis*. Note that the cell also has many chloroplasts (CH) and a large nucleus (N) but is lacking cell wall ingrowths. Some plasmodesmata (arrow) also occur on the walls between cells.

It is believed that the leaves of seagrasses have the capacity to take up nutrients from surrounding water (Arber, 1920; Sculthorpe, 1967; Raven, 1981). Using radioactive isotopes the uptake of carbon (Harrison, 1978; Barbour and Radosevich, 1979), phosphorus (McRoy and Barsdate, 1970), cadmium (Faraday and Churchill, 1979; Brinkhuis *et al.*, 1980) and manganese (Brinkhuis *et al.*, 1980) by the leaf has been demonstrated for several seagrasses. However, there are no similar studies on Australian seagrasses.

Mesophyll Cells and Air-lacunae: Mesophyll cells of seagrasses are thin-walled but highly vacuolated. The thin peripheral cytoplasm contains few chloroplasts with small starch granules. The mesophyll cells surround air lacunae of varying size (Fig. 2, **A-G**) and in some genera (e.g. *Zostera*) the surface area of air lacunae may occupy half of a leaf surface area in cross section (Fig. 2, **D**). It has been shown that the air lacunae contain oxygen and carbon dioxide (Zieman, 1974). The storage of these gases in the air lacunae could swell the leaf blades of *Thalassia testudinum* up to 200–250% during the day (Zieman, 1974). The presence of air lacunae has been considered important in seagrass photosynthesis, particularly in re-fixation of carbon dioxide. Oxygen produced in photosynthesis could build up in these lacunae, and respiratory and photorespiratory carbon dioxide could diffuse into them as well. Zelitch (1971) estimated that up to 50–67% of photorespired carbon dioxide in *T. testudinum* leaves was recycled.

Z. *muelleri* grows in both intertidal and subtidal mudflats in Westernport Bay, Victoria. The surface area of air-lacunae in the leaves of the intertidal form is only about one-third that in the leaves of the subtidal form (Kuo, in preparation). This finding correlates well with the photosynthesis rate in this species. Clough and Attiwill (1980) found that the photosynthesis rate of the subtidal form is about three times that of the intertidal form.

There are many septa interrupting the air-lacunae along the leaf. Each septum consists of a group of small parenchyma cells with minute pores at their intercellular spaces. Numerous external wall ingrowths projecting into these pores are present in the septa of *Zostera muelleri* and *Z. capricorni* but are absent from those of more than twenty seagrass species belonging to twelve genera examined so far (Kuo, in preparation).

Vascular System: In general, each vascular bundle is surrounded by a layer of sheath cells (Fig. 4, **B, E**), though Benedict and Scott (1976) could not distinguish sheath cells in *Thalassia testudinum*. The sheath cells of *Posidonia* have a thin but lignified wall (Kuo, 1978), those of *Syringodium* have suberin lamellae in the wall, those of *Thalassodendron* and *Amphibolis* have a thick but not lignified wall and those of *Zostera* and *Heterozostera* have cell wall ingrowths (Kuo, unpublished). The vascular sheath cells of seagrasses therefore appear to have the potential to regulate solute movement between the mesophyll and the vascular tissues, but this has never been demonstrated experimentally.

The number and size of xylem elements in the vascular bundles of seagrasses, as well as in other aquatic plants, are much reduced in comparison with terrestrial plants (Sculthorpe, 1967). Xylem walls in seagrasses have little lignification and secondary wall thickening (Kuo, 1978; Fig. 4, **D, G**). The reduced xylem has led some researchers to suggest that there is little xylem transport in seagrasses (e.g. Tomlinson, 1972), but precise experimental work on this point appears to be lacking. The structure of the phloem tissues in seagrasses is similar to that of terrestrial plants. Sieve tubes of *Posidonia* contain a plasmalemma, endoplasmic reticulum, mitochondria and plastids but lack nuclei (Kuo, 1978; Fig. 4, **G**). Companion cells are rich in cytoplasm. Sieve
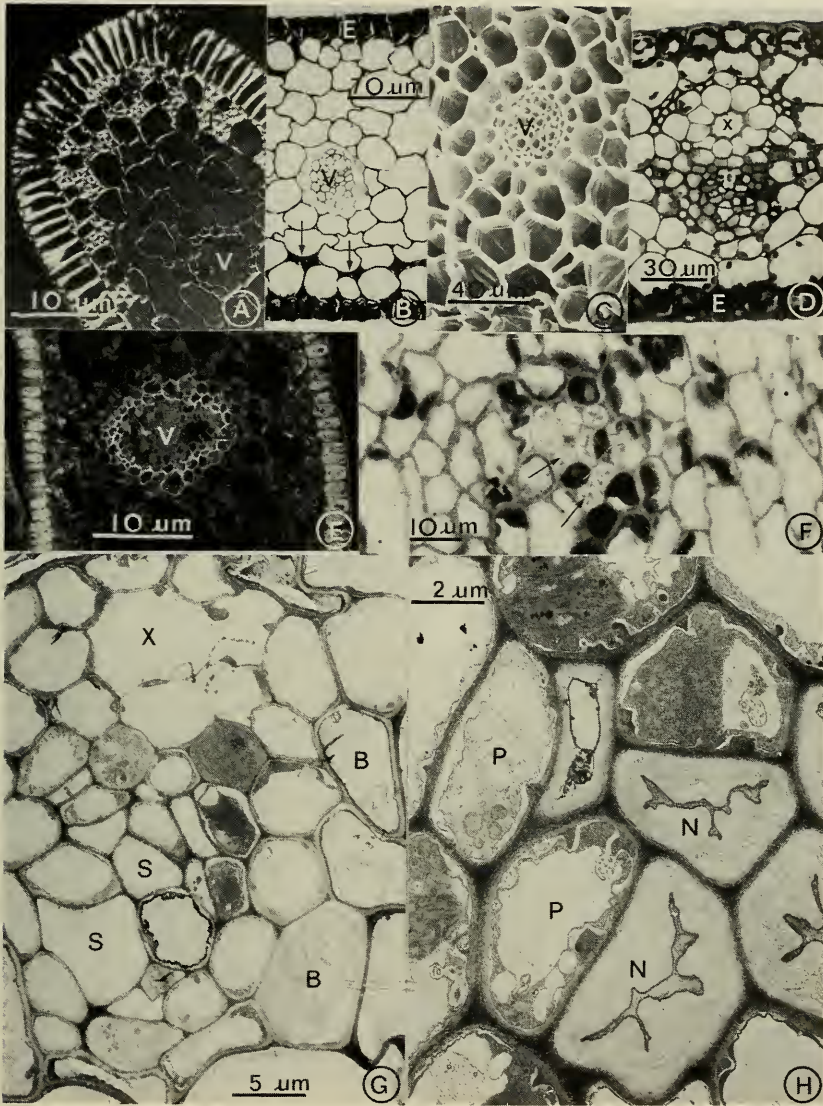
Fig. 4. The leaf vascular structure in some Australian seagrasses.

A. A polarizing micrograph of *P. australis* leaf blade. Notice that the cell walls of the epidermal and fibre cells are intensively birefringent but that of vascular bundle (V) is not so.

B. The sheath cells of vascular bundle (V) in *P. sinuosa* is not so intensively stained with PAS reaction. Fibre cells (arrows) occur between the epidermal (E) and the hypodermal cells.

C.(SEM) and **D**. The vascular bundle (V) of *Z. muelleri*. Note that a single xylem lacunae (X) separates from the phloem tissue (P). Fibre cells associated with vascular tissue but not with the epidermal cells (E).

E. Both the epidermal cell contents and the sheath cells of the vascular bundle (V) in *P. australis* leaf blade are strongly autofluorescent.

F. Nacreous wall sieve elements (arrows) are found in the vascular bundles of *H. tasmanica* leaf sheath.

G. Electron micrograph of the vascular bundle in *P. australis* leaf blade. Note that the bundle is surrounded by a layer of lignified sheath cells (B). The walls of xylem elements (X) are poorly secondary thickness and weakly lignified and that of sieve tubes (S) and of parenchyma cells are normal.

H. Nacreous wall sieve tubes (N) and cell wall ingrowths in parenchyma cells (P) occur in the vascular bundle of *Z. muelleri* leaf blade.

tubes of the family Zosteraceae and the sole genus *Halodule* of the family Cymodoceacae have nacreous or thick walls with reduced lumens and the companion cells of these species have cell wall ingrowths (Kuo, 1983; Fig. 4, **F, H**). The reduction of lumen area in nacreous sieve elements relates to the translocation rate and has received little attention in terrestrial plants (Esau and Cheadle, 1958).

Mechanical Tissues: The prominent fibre cells (Fig. 3, **A, C**; Fig. 4, **B**) of the leaves are of particular interest. Mechanical tissues occur only in the leaves of certain genera, they may be associated with vascular bundles (e.g. *Zostera*) or distributed among parenchyma tissue (e.g. *Posidonia*). They have thickened walls, which consist of pectin and cellulose but do not contain lignin (Kuo, 1978). Thus they could provide tensile strength but retain a high degree of flexibility, allowing the leaves to withstand vigorous ocean wave action. The distribution of these fibre groups in the leaves of *Posidonia* can be used as a taxonomic character (Sauvageau, 1890; Cambridge and Kuo, 1979).

2. LEAF SHEATH (Fig. 5).

The leaf sheath encloses the basal portion of the leaves and usually lies beneath the sediment surface (Fig. 5, **A**). The anatomy and cellular structures of the sheath of *Posidonia* differ markedly from the blade (Kuo, 1978; Fig. 5, **B, C**). The cuticle is electron-transparent and is not porous. A thin lignified or suberized layer is present on the outer wall of abaxial epidermal cells. This layer or the cuticle may act as a physical barrier between the inner developing leaf tissue and surrounding water. Tyerman (1979, personal communication) reported that the sheath may function to maintain a relatively low osmotic pressure for the leaves meristem of *P. australis*. In contrast to the blade the sheath epidermal cells of *Posidonia* lack chloroplasts and are highly vacuolated with a thin peripheral cytoplasm. The structure of vascular bundles is similar to those in the blade. Groups of fibre bundles are widely distributed among the parenchyma tissues of the sheath (Kuo, 1978; Fig. 5, **B**) but in contrast to the fibre bundles of the blade, they are lignified and because of this they persist on the rhizomes long after the other tissues of the leaf sheath have rotted away (Fig. 5, **A**). The sheath fibres of *Posidonia* can be deposited both beneath living seagrass meadows and on ocean floors bordering the coast (Kuo and Cambridge, 1978). Deposits of these marine fibres in Spencer and St Vincent Gulfs in South Australia are present in such quantities that the fibres were harvested over a limited period (1905 to 1915) for grain bags, paper making and insulation material (Winterbottom, 1917; Reid and Smith, 1919).

3. STEM AND RHIZOME (Fig. 5).

In transverse sections, both erect stem and rhizomes of *Amphibolis, Zostera* and *Thalassodendron* exhibit similar morphological features (Ducker *et al.*, 1977; Fig. 5, **D, E, G**). The central stele has a central xylem surrounded by phloem bundles (Fig. 5, **E**). The stele is surrounded by the cortex in *Posidonia* or by aerenchyma in *Amphibolis, Thalassodendron* and *Zostera*. Two distinct cortical zones can be recognized in *Amphibolis* and *Zostera* based upon morphological and histochemical characters. Starch grains are prominent in the cortical cells of *Posidonia* rhizomes, and groups of lignified fibre cells are scattered through the cortex of *Posidonia* rhizomes (Kuo and Cambridge, 1978; Fig. 5, **G**). A few peripheral vascular strands are distributed among the cortical tissues (Fig. 5, **E**). The distribution and number of vascular strands appear to be a species characteristic (den Hartog, 1970; Ducker *et al.*, 1977). A distinct cuticle covers both stem and rhizome. Cell walls of the epidermal and hypodermal cells are thickened and lignified and sometimes these cells contain polyphenolic materials (Fig. 5, **F**). A few
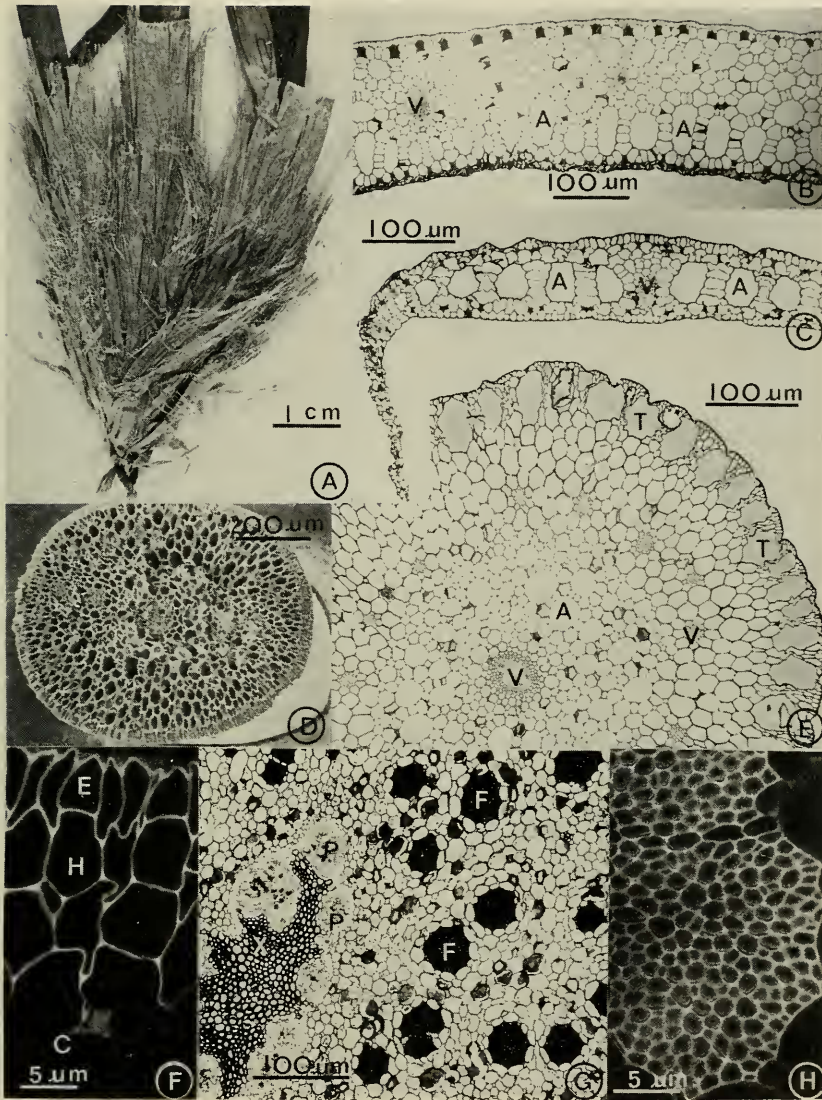
Fig. 5. The anatomy and the leaf sheaths and rhizomes in seagrasses.

A. Old leaf sheaths of *P. australis* contain numerous fibres.

B and C. Transverse sections of the leaf sheaths of *P. australis* and *Z. muelleri* respectively. Many air-lacunae (A) occur in both species but *P. australis* has more fibre bundles among the parenchyma tissue. V: vascular bundles.

D. A scanning electron micrograph of a *P. australis* rhizome in a transverse view.

E. A transverse section of *Syringodium isoetifolium* rhizome shows numerous vascular bundles (V), air-lacunae (A) and large tannins-containing cells (T) but there are no fibre bundles in the rhizome.

F. The cell walls of both the epidermal (E) and the hypodermal cells (H) of *P. australis* rhizome are autofluorescent but those of the cortical cells (C) are not.

G. Transverse section of *P. australis* rhizome showing the central stele has a xylem element (X) surrounded by numerous phloem bundles (P), many large fibre bundles scatter among the cortical tissue which contains numerous minute starch granules.

H. A higher magnification of a fibre bundle in *P. australis* rhizome showing the middle lamellae of the fibre cells are autofluorescent.

bacteria and diatoms are often present on the surface of rhizomes and numerous epiphytic algae occur on the stem.

4. ROOTS (Fig. 6).

Both rhizomes and roots serve as anchor systems for seagrasses. The external morphology of roots may vary between species and appears to be associated with their ecological habitat and mineral nutrient environment. For example, the roots of *Halophila* and *Zostera* are creamy in colour and soft, with many root hairs, and appear to be suitable for survival on soft substrates. *Posidonia* roots are thick but relatively soft with many branches; the root hairs are sparse, and the plants live on the sandy ocean floor (Figs 1, 6, **A**). Hard, wavy and branched roots are usually found in *Amphibolis*, and appear suitable to anchoring on harder substrates such as rocks or marine fibres. The roots of *Thalassodendron* are thick and strong, with shiny black surface roots, and have few branches. These roots apparently penetrate the interstices of the rocky substrates and anchor the plants against the turbulence of ocean waves. The anatomy of the roots, however, appears to be very similar among the species. All roots have a distinct root cap (Fig. 6, **B**). The central stele (Fig. 6, **C-E**) consists mainly of well developed phloem and a central weakly lignified xylem, and is surrounded by an endodermis which has a Casparian strip in the radial cell wall (Kuo and Cambridge, 1978; Fig. 6, **H**). Cortical cells are thin-walled and may have many large air-lacunae. Cell walls of the epidermal cells and three to four layers of hypodermal cells are thickened and lignified in harder roots, such as those of *Thalassodendron, Amphibolis* and *Posidonia* (Fig. 6, **F**). The thickened hypodermal walls may have suberin lamellae (Kuo and Cambridge, 1978; Fig. 6, **I**). Nutrients are taken up by roots and rhizomes of seagrasses from the sediment and are transported to all parts of the plant. Directions and rates of nutrient transport are likely to be dependent upon the morphology, age and physical condition of the individual plants as well as the species. This translocation probably occurs in the xylem and phloem of the vascular system. However, McRoy and Barsdate (1970) showed that the leaves and stems of *Zostera marina* L. absorbed more phosphorus than did the roots and rhizomes. Wetzel and Penhale (1979) found the rates of carbon uptake and transport from roots and rhizomes to the leaves of *Halodule wrightii* Aschers. are much higher than those for *Zostera marina* and *Thalassia testudinum*. Thus it appears that both leaves and roots of seagrasses may have the capacity to take up nutrients, although the quantitative role in nutrient uptake in a natural environment is still unknown. Data on nutrient uptake by Australian seagrasses are still not available.

LIFE HISTORY

Some seagrasses appear to show infrequent flowering. *Cymodocea serrulata* flowers have been recorded once, and these were male (Kirkman, 1975) while Tomlinson (1969) observed an average arrangement of male:female shoot ratio of 4:1 for *Thalassia testudinum* in Florida. Other species show regular flowering and some have the male and female flowers on the same shoot — e.g. *Posidonia australis* whose flowers are initiated in autumn when day lengths are shortening and temperatures are falling, and the flowers open in spring (Cambridge, 1975).

Aspects of floral morphology and development in seagrasses have been investigated only for some members of the family Cymodoceaceae (Isaac, 1969; Kay, 1971; Ducker *et al.*, 1978; Tomlinson and Posluszny, 1978). But this information is lacking for other families of seagrasses, probably due to the difficulty of obtaining material. *Posidonia* flowers (Fig. 7, **A**) are bisexual with a perianth. Mature pollen grains of most seagrass species are thread-like with a pair of fine curved hooks at the
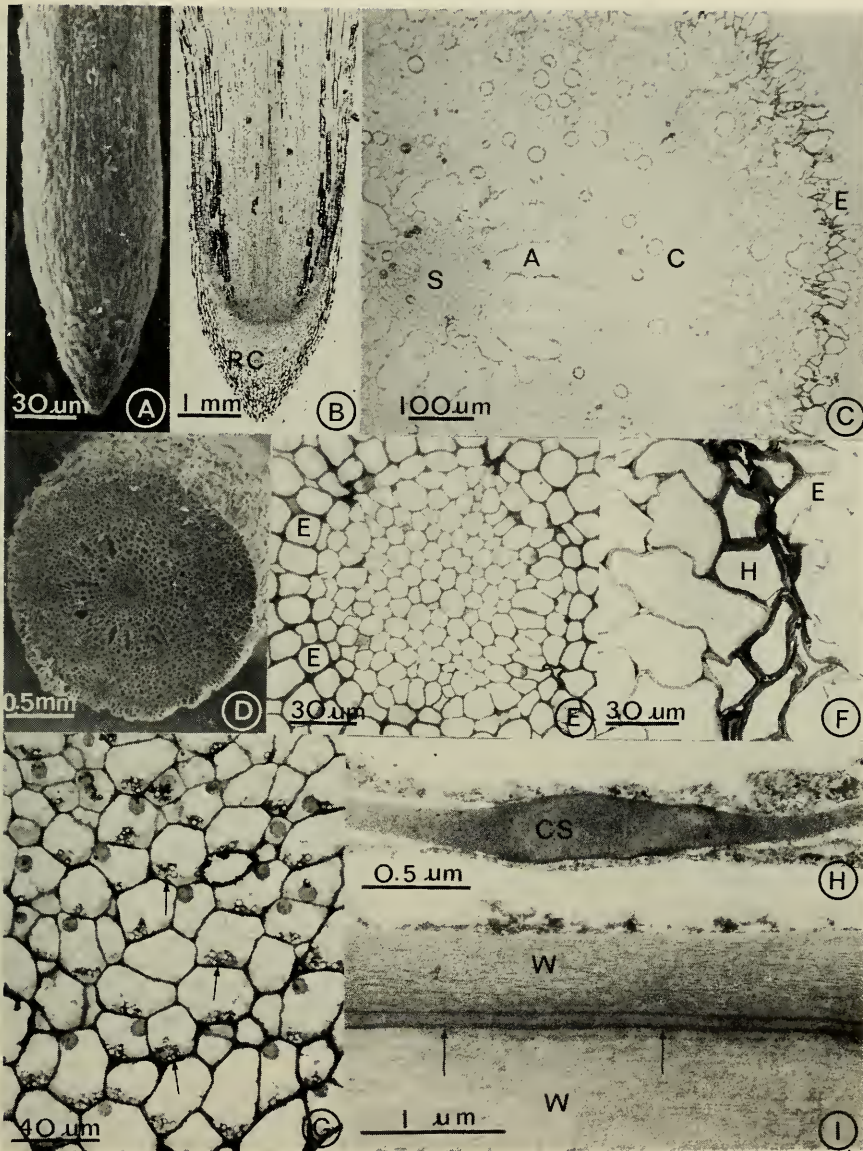
Fig. 6. The anatomy of *P. australis* roots.

A. A scanning electron micrograph of a mature root.

B. A median longitudinal section of a mature root tip with a pronounced root cap (RC).

C. A transverse section of a mature root showing the stele is surrounded by a series of air-lacunae (A), many thin-walled cortical cells (C) and a layer of the thin-walled epidermal cells (E).

D. A scanning electron micrograph of a mature root in a transverse view.

E. A high magnification of a stele with a distinct layer of endodermis (E).

F. A high magnification of the root periphery showing that the thin-walled epidermal cells (E) with thicker-walled hypodermal cells (H).

G. Numerous starch granules (arrows) are located in the basal portion of the root cap cells.

H. A distinct Casparian strip (CS) is present in the radial walls of two adjacent endodermal cells.

I. Electron dense suberin lamellae (arrows) are present in thickened walls (W) of the adjacent hypodermal cells.

end (Pettit and Jermy, 1975; Pettit, 1976, 1980; Ducker *et al.*, 1978; Fig. 7, **B**), probably for attachment to the stigma surface. In contrast to terrestrial flowering plants, the pollen of seagrasses lack an exine or it is poorly developed (Fig. 7, **C, D**). The pollen is released under water and drifts about submerged. The mechanism of seagrass pollination has been discussed elsewhere (Ducker and Knox, 1976; Ducker *et al.*, 1978; Pettit, 1980). Enzymatic properties of the pollen wall and stigma pellicle in seagrasses are comparable with those found in terrestrial flowering plants. Pettit (1980) suggested a similar mechanism of cuticle erosion in both pollen grain and stigma might well follow compatible pollination both on land and in the sea.

The fruits of *Posidonia* mature about three months after anthesis (Fig. 7, **E, F**). Cambridge (1975) estimated that *P. australis* in Cockburn Sound, Western Australia, may produce 500 fruits per square metre of meadow. Each seed is enclosed by a thin membrane which resembles the seed coat of terrestrial plants, and then by a pericarp which has a well-developed aerenchyma system. The bulk of the seed consists of en-dospermic tissue which serves as nutrient storage. Starch and lipid are the main nutrient reserves and storage protein is lacking. Nitrogen, phosphorus and other macro-and micro-elements occur in concentrations which are in general comparable to those of terrestrial plants (Hocking *et al.*, 1980). Mature fruits with their pericarps are released in summer and float to the water surface. After a day or two the pericarp ruptures and the seeds sink to the floor of the sediment (Fig. 7, **G**). Germination may begin even before the seeds are released from the pericarp. The young seedlings (Fig. 7, **H**) may depend upon the nutrient storage of the seed up to nine months after germination (Hocking *et al.*, 1981).

In *Amphibolis* and *Thalassodendron* the germination of the seed is viviparous. The flowers of these seagrasses occur on separate plants in summer. The fruits develop at the apices of the lower branches of female plants. Mature embryos burst through the apices of their pericarps and appear as little seedlings, which continue their growth on the parent plant for some time (Fig. 7, **I**). The seedlings, with cup-like pericarp structures, are released from the parent plants in winter and float in the ocean. Finally, the seedlings become anchored in the sediments or to the bases of plants in meadows by the comb-like lobes of the upper pericarp. Then the stems begin to grow rapidly and later shoots produce rhizomes with roots.

Cambridge and Kuo (in press) describe an unusual form of vegetative propagation in *Heterozostera tasmanica*. Small propagules develop in the non-fertile erect stems of the parent plant during spring and summer. Eventually, erect stems carrying propagules break off from the parent plants and drift away. These propagules may then find a suitable location for further development.

Although the rate of leaf production in an established seagrass meadow has been estimated (West and Larkum, 1979; Cambridge, 1981), little is known about either the rate of underground tissue production or the growth rate from a seedling to its maturity in any seagrass. Old leaves of *Posidonia* plants usually break off at the junction between the blade and sheath in autumn and leaf litter from seagrass may accumulate as high as two metres along some parts of the south-west Australian coastline during the winter. It is washed back into the ocean by late spring. There is no doubt that seagrasses are playing an important role in marine food chains.

RHIZOME BRANCHING

Despite the large numbers of seeds produced, seagrass seedlings have been in-frequently observed in the field and vegetative propagation by growth of rhizomes is probably of greater importance in the maintenance and spread of seagrasses than is seed production (Tomlinson, 1974).
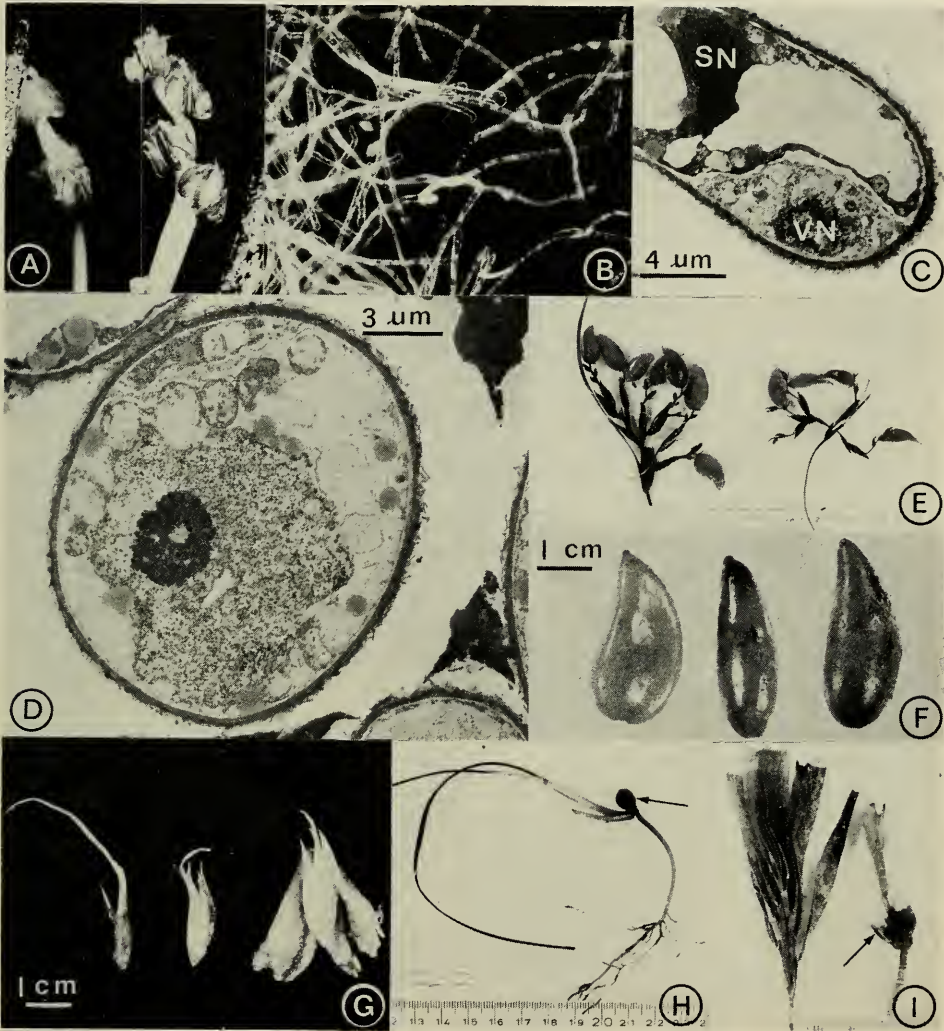
Fig. 7. Flowers, pollen grains, fruits and germination in seagrasses.
A. Flowering in *P. australis*.
B. Thread-like pollen grains of *P. australis*.
C and D. Electron micrographs of pollen grains of *P. australis* showing that pollen has both sperm (SN) and vegetative (VN) nucleus but lacks exine on the walls.
E. Fruits of *P. australis*.
F. Seeds of *Posidonia* (left: *P. ostenfeldii;* centre: *P. sinuosa;* right: *P. australis*).
G. Three germinating stages in *P. australis*. Note that there are no roots in the seedlings.
H. Six-months old seedling of *P. ostenfeldii*. Note it bears many leaves and roots, however, the seed (arrow) appear still intact.
I. A young (viviparous) seedling of *Amphibolis antarctica* showing a cup-shaped modified pericarp (arrow) attached to the stem of the parent plant.

An excellent study on rhizome branching systems in seagrasses was made by Tomlinson (1974). He found rhizome branching in some genera (e.g. *Amphibolis, Thalassodendron, Heterozostera*) is sympodial and in others (e.g. *Posidonia, Zostera, Cymodocea,* etc.) is monopodial. The branching sequence may be (a) continuous (i.e. branch at every node, *Syringodium, Halophila*); (b) diffuse (i.e. branches produced at irregular intervals, *Posidonia, Zostera*, etc.) or (c) periodic (i.e. branches produced at regular intervals (*Thalassia*). In addition to relative uniformity of the marine environment, the success of vegetative growth rather than propagation from seed in seagrasses could result in a low frequency of sexual recombination and, consequently, in a slow rate of evolutionary change. It is possibly for these reasons that *Posidonia oceanica* (L.) Delile from the Mediterranean is similar to *P. australis* of Australia, and *Thalassia testudinum* of the Caribbean is closely related to *T. hemprichii* of tropical Indo-Pacific regions. The species in both cases appear to have diverged relatively little since they were originally separated from one another in the Miocene (den Hartog, 1970).

PHYLLOSPHERE AND RHIZOSPHERE

Phyllosphere. Seagrass leaves bear varying numbers of epiphytes, depending upon age, season and environmental conditions. The epiphytes include bacteria, diatoms, algae (Fig. 8, **A-E**), and animals or 'zoo-epiphytes' such as hydroids (Fig. 8, **F**), sponges, etc. In general the older portions of the leaf support more epiphytes, and sometimes epiphytes may occlude half of the leaf area of a seagrass standing crop (Fig. 8, **I**). Even on the surface of newly emerged leaf blades there are numerous bacteria and diatoms (Fig. 8, **A, B**). As far as the abundance of epiphytic algae in Australian seagrasses is concerned, more than twenty species have been found on *Posidonia australis* from Kangaroo Island, South Australia (Womersley, 1956); more than fifty species were found on *Zostera capricorni* Aschers., *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog, and *P. australis* in Botany Bay and Jervis Bay, New South Wales (May *et al.*, 1978); Ducker *et al.* (1977) have recorded more than one hundred species of epiphytic algae on *Amphibolis* around Australia. The level of salinity may affect the growth of epiphytes. Den Hartog (1970) noted that *P. australis* from the high salinity areas such as the sea inlets in the Sydney area and Shark Bay in Western Australia have considerably fewer epiphytes than *P. australis* from an open sea.

The attachment of epiphytes to the host appears to be limited to the cuticle of the host (Fig. 8, **G**) though Ducker and Knox (1978) have observed the red alga *Heteroderma cymodoceae* to erode locally the cuticle and outer wall of the epidermal cells of *Amphibolis antarctica* stems.

Epiphytes could reduce seagrass photosynthetic rates by acting both as a barrier to carbon dioxide uptake and by reducing light intensity (Sand-Jensen, 1977; Cambridge, 1979). On the other hand, seagrasses may be able to reduce their epiphyte stands by producing new photosynthetic tissues, or perhaps by excreting toxic substances (Sand-Jensen, 1977).

The transfer of nutrients between epiphytic algae and *Thalassia testudinum* has been demonstrated (Goering and Parker, 1972; Harlin, 1973; McRoy and Goering, 1974).

Rhizosphere. The roots of seagrasses could also provide an environment for micro-organisms. The micro-organisms in the rhizosphere may play an important role in aiding nutrient uptake, affecting pathogen invasion and in nitrogen fixation. Numerous bacteria and other micro-organisms have been found in the rhizospheres of several seagrass species (Kuo *et al.*, 1981; Fig. 8, **H**), and appear to penetrate only the periphery of the host tissue. However, it is still not known whether those micro-organisms are able to fix nitrogen. Patriquin (1972) hypothesized that bacterial
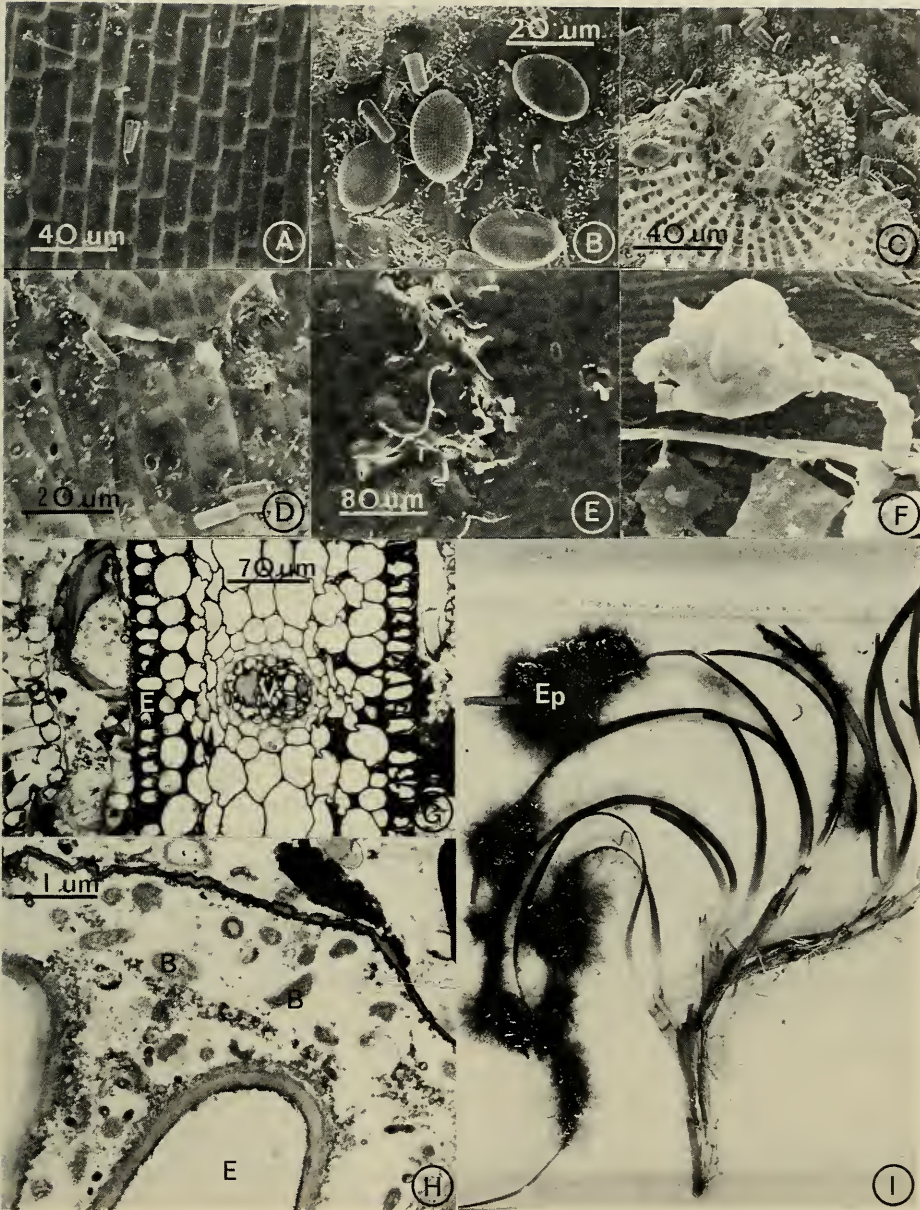
Fig. 8. Epiphytes and rhizosphere in seagrasses.
A-D. Scanning electron micrographs show various epiphytes associated with the leaf blade of *P. ostenfeldii*.
A, numerous bacteria; B, bacteria and diatoms; C, bacteria, diatoms and calcareous red algae; D, bacteria, diatoms and unknown organisms had damaged the epidermal surface.
E. A fungal hyphae-like structure on the leaf blade of *P. australis*.
G. A transverse section of *P. sinuosa* leaf blade showing numerous epiphytes are present on the leaf surface (V: vascular bundles; E: epidermal cells).
H. Electron micrograph of *P. australis* rhizosphere showing some bacteria located on the outer surface of root epidermal cells (E).
I. Numerous algae epiphytes (Ep) in association with the leaf blades of a *P. australis* plant.

nitrogen fixation probably operated in seagrass rhizospheres, and Patriquin and Knowles (1972) provided experimental support. However, McRoy *et al.* (1973) could barely detect C_2H_2 reduction associated with sediments, roots, rhizomes or leaves of *Thalassia testudinum*. Capone *et al.* (1979) found that dead leaves of *T. testudinum* have only one third of the nitrogen concentration of green leaves, and they estimated bacterial nitrogen fixation in the sediments supplied up to a quarter to half of the nitrogen required for leaf production.

Concluding Remarks

Seagrasses are abundant in Australian waters and many of them are endemic. Investigation of the biology of Australian seagrasses is still in an early stage. Natural habitats of seagrasses should be more carefully studied. Seagrasses have yet to be collected from the north-west of this continent to map Australian species completely. A critical but comprehensive taxonomic study of Australian seagrasses, particularly in the genera *Halophila, Posidonia* and *Zostera* is urgently needed. The storage of seagrass specimens in liquid as well as dehydrated states in herbaria is highly desired. Some structures of seagrasses are similar to those in terrestrial plants, while others are specialized adaptations in a marine environment. The development of various vegetative and reproductive structures as well as germination in seagrasses is not well understood. A combined biochemical, physiological and structural study on seagrasses in relation to nutrient uptake, photosynthesis, translocation and transportation is required. The relationship between epiphytes, zoo-epiphytes, rhizosphere and seagrasses also requires more attention.

Acknowledgements

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